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TUMIDOTHERES, A NEW GENUS FOR PINNOTHERES MARGARITA SMITH, 1869, AND PINNOTHERES MACULATUS SAY, 1818 (BRACHYURA: PINNOTHERIDAE)

Ernesto Campos

ABSTRACT

The genus *Tumidotheres* is erected to receive its type species *Pinnotheres margarita* Smith, 1869, from the East Pacific, and *P. maculatus* Say, 1818, from the West Atlantic. It differs from other pinnotherid genera principally in 3 features: (1) the gastric and cardiac regions are separated from the branchiohepatic area by depressions, all these regions tumid; (2) the palp of the third maxilliped is composed of 3 articles, with the carpus shorter than the spatulate propodus, the dactylus narrowly spatulate, inserted medially on the propodal inner margin and not overreaching the tip of this latter article; and (3) male and female abdomen composed of 7 free abdominal somites. An analysis of morphology of several postplanktonic stages of T. (formerly *Pinnotheres*) margarita suggested that this species should be considered as a senior synonym of *P. pubescens* (Holmes, 1894), which apparently was described from a hard-stage female. In addition, the life history, phylogenetic relationships, and larval morphology of *Tumidotheres* are discussed.

RESUMEN

Un nuevo género de cangrejo pinotérido, *Tumidotheres*, genus novum, es nombrado para recibir a su especie tipo, *Pinnotheres margarita* Smith, 1869, del Pacífico oriental, y *P. maculatus* Say, 1818, del Atlántico occidental. Morfologicamente este género difiere de otros asignados a Pinnotheridae en tres características principales: (1) la región cardíaca y la gástrica están separadas del área branquio-hepática por depresiones, siendo todas estas regiones del caparazón túmidas; (2) el palpo del tercer maxilipedio está formado por tres artejos, el carpus más corto que el espatulado propodus y el dactilus, el cual es angostamente espatulado, está inserto en la región media del propodus y su extremo distal no sobrepasa la punta de éste último artejo; y (3) el abdomen del macho y de la hembra están compuesto por siete somitos libremente articulados. Adicionalmente se reconoce que *Pinnotheres pubescens* (Holmes, 1894) fue descrito en base a una hembra en fase dura de *T*. (ex *Pinnotheres) margarita* (Smith, 1869) la cual por haber sido descrita primero debe considerarse un sinónimo antiguo y el nombre válido para esta singular especie. Comentarios adicionales sobre el ciclo de vida, relaciones filogenéticas y morfología larval se discuten para *Tumidotheres* y géneros emparentados.

The pinnotherids are a group of symbiotic crabs that undergo a complex metamorphosis during their postplanktonic development. According to previous studies (Christensen and McDermott, 1958; Pearce, 1966; Jones, 1977) the male passes through two forms after the invasive stage: (1) the prehard-stage, which has a soft, bare carapace, with no swimming setae on the walking legs, and (2) the hard-stage, with a hairy, hard carapace and natatory setae on the second and third walking legs. In contrast, seven stages are recorded in the female. The first two, the prehard- and hard-stages, are nearly identical morphologically with the same stages observed in the male, and differ mainly in the number of abdominal appendages. The last five stages are feminine

forms that are termed the post-hard stages I-V. Differences among them have been recorded in carapace shape, abdominal width and length, and development of pleopods (Christensen and McDermott, 1958; Pearce, 1966; Jones, 1977). Changes in the symmetry of the walking legs and swimming setae can also be observed. The morphological changes that take place during the life history have been confused by taxonomists. This has resulted in the naming of two or more species that represented different stages of development in the same species (e.g., *Pinnotheres muliniarum* [=*P*. reticulatus = P. jamesi], Campos, in preparation).

During October 1984 I collected a swimming pinnotherid female in the upper Gulf

of California that was attempting to infest the vagile mollusc Lima pacifica Orbigny, 1846. Close examination of this crab and its comparison with the description of the eastern Pacific pinnotherid crabs by Rathbun (1918) indicated that I had captured a female of the enigmatic crab Pinnotheres pubescens (Holmes, 1894). One year later, additional collection of two solitary males, housed in *Lima pacifica*, and two sexual couples, found in the mantle cavity of Barbatia reeveana (Orbigny, 1846), allowed me to conclude that P. pubescens was described from a subadult female of P. margarita Smith, 1869. The solitary males and the males found together with the young females were almost identical to the male of P. margarita figured by Campos-González and Campoy-Favela (1988).

Furthermore, comparison of the morphology and life history indicates that *P. margarita* is closely allied to the western Atlantic *P. maculatus*, and that both species possess several morphological features that justify their exclusion from *Pinnotheres* sensu stricto and their inclusion in a new genus of Pinnotheridae.

DESCRIPTIVE ACCOUNT

Tumidotheres, new genus

Diagnosis. — Carapace suborbicular, broader than long, thick and firm but not hard; surface covered with short, dense, and deciduous tomentum. Gastric and cardiac regions separated from branchiohepatic area by depressions, all these regions tumid. Third maxilliped with ischium indistinguishably fused with merus; palp with 3 articles, carpus shorter than spatulate propodus, latter about twice as long as wide; dactylus narrowly spatulate, inserted in angular notch in middle of ventral margin of propodus, not extending beyond tip of propodus. Abdomen in both sexes with 7 free somites.

Type Species. – *Pinnotheres margarita* Smith, 1869, by present designation. Gender masculine.

Etymology.—From Latin *tumidus*, swollen, and *theres*, to emphasize the possession of gastric, cardiac, and branchiohepatic regions of the tumid carapace.

Taxonomic Remarks.-In addition to the

above-mentioned type species, the western Atlantic Pinnotheres maculatus must be assigned to this genus. Other species that perhaps could be included in this genus are: Pinnotheres guerini H. Milne Edwards, 1853 (Cuba and Puerto Rico), P. hirtimanus H. Milne Edwards, 1853 (Cuba), P. leleouffi Crosnier, 1969 (Côte d'Ivoire, West Africa), and P. tellinae Manning and Holthius, 1981 (Pointe Noire, Congo). The latter four species do not agree with Pinnotheres sensu stricto and should be excluded from that genus. A morphological study is necessary to resolve the taxonomic position and systematics of these particular species, which possess a third maxilliped similar to that of Tumidotheres.

Generic Relationships. - Excluding those genera that possess the third maxilliped with palp articles placed end to end, and those which are morphologically similar to Pinnixa White, 1846, the genus Tumidotheres can be separated from the remaining genera in the Pinnotheridae by the unique structure of the third maxilliped (Fig. 2a, b). It is different from Pinnotheres sensu stricto by the form of the palp. Tumidotheres possesses a spatulate dactylus inserted in the middle of the propodus, and *Pinnotheres* sensu stricto possesses a styliform dactylus inserted proximally on the ventral margin of the propodus. The dactylus of Tumidotheres differs from that of Fabia. In Fabia the dactylus is lunate-digitiform and there are two longitudinal sulci on the carapace. These sulci are lacking in *Tumidotheres* and, as was noted above, its dactylus is spatulate. In addition, males of *Tumidotheres* possess seven free abdominal somites, instead of two or more fused as observed in males of Fabia (Campos, in preparation).

A comparison of adult and larval morphology indicates that *Tumidotheres* is more closely related to *Pinnaxodes* than to any other genus in the Pinnotheridae. As adults, both genera show a similar carapace shape, an abdominal configuration that is almost identical, and walking legs that are of a similar relative length. Differences are observed in the outer maxilliped. The ischium of *Pinnaxodes* is generally separated from the merus, while these articles are indistinguishably fused in *Tumidotheres*. Furthermore, in the former genus the dactylus extends beyond the tip of the propodus, while this article in Tumidotheres reaches almost to the tip of the propodus. Larval morphology has been compared by Hong (1974), who found that the larvae of Pinnaxodes major and T. maculatus are almost identical. The shape and number of carapace spines, abdominal somites, telson shape, and the antennae are very similar in both species. Furthermore, the number of articles of the maxillule, maxilla, maxillipeds, the setation on these appendages, and the number of zoeal stages are exactly the same. This close similarity in adult and larval morphology supports the hypothesis that Tumidotheres is phylogenetically allied to Pinnaxodes, and similar arguments also can be used to establish that both genera are not closely related to any other known genera in the Pinnotheridae.

Life History Remarks. - Based on a review of the available information on life histories of pinnotherid species and on my unpublished observations, I can recognize two patterns of reproductive behavior. In the first pattern (Christensen and McDermott, 1959; Jones, 1977) males and females in the hardstage live and copulate within the first and definitive host. The female molts and develops from the masculine form (hard-stage) to the feminine form (posthard-stage). The male also molts but remains in the hardstage. In the second type of reproductive behavior (Pearce, 1966, 1969), the crab infects an intermediate host after completing postplanktonic development. In this host the crab molts to become either the male or female hard-stage. This stage, which possesses long feathery natatory setae, leaves the intermediate host and participates in a copulatory swarming in the open sea. Afterward, the female, and eventually the male, infect the definitive host. The female molts several times and develops to the ovigerous stage; the male molts and grows but remains in hard-stage. This second type of reproductive behavior has been documented for T. maculatus and Fabia subquadrata, and preliminary observations permit me to infer that T. margarita possesses a similar behavior.

In my opinion the finding of the above divergent reproductive behaviors, which are closely related to functional morphology and suggest divergent evolutionary trends, gives additional support to the establishment of the genus *Tumidotheres*.

Tumidotheres margarita (Smith, 1869), new combination Figs. 1–3

- Synonymy.—Pinnotheres margarita Smith, 1869: 245.—Smith, 1870: 166–169.—Lockington, 1877: 154.—Miers, 1886: 276.—Holmes, 1894: 564.— Rathbun, 1910: 587, 1918: 91–93.—Tesch, 1918: 285–286.—Glassell, 1934: 301.—Silas and Alagarswami, 1967: 1178, 1202, 1223, 1225.— Schmitt, McCain, and Davidson, 1973: 5, 9, 56, 57.—Wicksten, 1982: 221–225, fig. 1.—Campos-González, 1988: 385.—Campos-González and Campoy-Favela, 1988: 221–225, figs. 1, 2.
- Cryptophrys pubescens Holmes, 1894: 564, 565, pl. 20, figs. 6, 7.
- Pinnotheres pubescens (Holmes, 1894): Rathbun, 1918: 63, 65, 66, 87, 88, fig. 43.-Glassell, 1934: 301.-Schmitt, McCain, and Davidson, 1973: 82.

Material Examined.-GULF OF CALIFORNIA.-Laguna Percebú, about 23 km south of San Felipe, Baja California, 1 young 9, 9 October 1984, E. Campos, collector, host Lima pacifica Orbigny, 1846; 2 88 and 2 young 99, 20 November 1985, E. Campos, coll., host Barbatia reeveana (Orbigny, 1846). Puertecitos, km 72, road San Felipe-San Luis Gonzaga, Baja California, 2 young 88, 13 September 1985, G. Lopez and E. Campos, coll., host L. pacifica. Playa Kino Viejo, Sonora, 2 99 (1 ovigerous), 24 January 1985, J. R. Campoy-Favela, coll., from Argopecten circularis (Sowerby, 1835). Punta San Pedro, Bahía Concepción, Baja California Sur, 1 ovigerous 9, May 1983, P. A. Ramirez, coll., host Pinctada mazatlanica (Hanley, 1855); 1 9, 18 May 1984, P. A. Ramirez, coll., host P. mazatlanica; 3 99 (2 ovigerous), 4 November 1984, J. L. Bello-León, coll., host P. mazatlanica. WEST COAST OF BAJA CALIFORNIA.-Estero El Cardon, Laguna de San Ignacio, Baja California Sur, 4 88 and 30 99, 4 April 1987, Eulogio Lopez, coll., host Argopecten (?) aequisulcatus (Carpenter, 1864). Agua Blanca, Bahía del Rosario, Baja California, 1 º, 4 April 1986, A. Salas, coll., host Hinnites giganteus (Gray, 1825).

Distribution. – West coast of Baja California north to Bahía del Rosario, Baja California; Golfo de California, from Laguna Percebú, about 23 km south of San Felipe, Baja California, to La Paz, Baja California Sur, and Bahía Kino, Sonora to Bahía de Panamá (Campos-González, 1988; present study).

Hosts. – Mollusca: Bivalvia. Argopecten circularis (Sowerby, 1835), Hinnites giganteus (Gray, 1825), Argopecten (?) aequisulcatus (Carpenter, 1864), Pinctada mazatlanica (Hanley, 1855), Lima pacifica Orbigny, 1846, Barbatia reeveana (Orbigny, 1846) (see Campos-González, 1988; present study).

Subadult Female. - Body and legs with short



Fig. 1. Female of *Tumidotheres margarita* (Smith, 1869). Carapace width = 7 mm. a, dorsal view; b, frontal view.

pubescence. Carapace subpentagonal (Fig. 1a) convex, front projected, notched in middle; postfrontal ridge extending over full width of carapace; gastric and cardiac regions tumid and separated from hepatic and branchial regions by longitudinal depression; slight depression between gastric and cardiac regions, another depression behind it.

Third maxilliped obliquely placed in buccal cavity (Fig. 1b); ischium and merus indistinguishably fused, inner margin angulate at middle; palp of 3 articles, carpus shorter than propodus, latter subspatulate,



Fig. 2. Tumidotheres margarita (Smith, 1869). Female, carapace width = 7 mm. a, third maxilliped; c, chela; d, left leg; e, right leg; f, abdomen. Line around female abdomen indicates marginal feathery hairs. Male, carapace width = 3.7 mm. b, third maxilliped.



Fig. 3. Degree of development of the right first pleopod of the male of *Tumidotheres margarita* (Smith, 1869). a, immature male, carapace width = 3.5 mm, cephalic view; b, immature male, carapace width = 3.7 mm, abdominal view; c, mature male, carapace width = 6.6 mm, abdominal view.

widest in middle at insertion of dactylus; latter narrowly spatulate, reaching almost to tip of propodus (Fig. 2a, b).

Chelipeds stouter than walking legs; chela slightly increasing in height distally (Fig. 2d, e); palm with subpyramidal elevation on inner face and convex on outer face; fingers shorter than palm, hooked at tip; dactylus slightly longer than pollex, with triangular tooth and notch proximally placed on cutting edge; pollex slightly deflexed, with smaller teeth on cutting edge.

Walking legs moderately stout, each pair symmetrical in length except second one, with left dactylus slightly longer than that on right; propodus of leg 1 with feathery swimming setae along ventral margin; carpus and propodus of legs 2 and 3 with 2 fringes of long feathery setae placed on outer face, third fringe up ventral margin on inner face; dactyli slender and curved; fourth dactylus longer and less curved than preceding ones. In decreasing order, relative length of walking legs 2 > 3 > 4 > 1.

Abdomen orbicular (Fig. 2f), slightly longer than broad, laterally not reaching coxae of walking legs, distally reaching notch of first thoracic sternite; margin clothed with long feathery setae.

Pinnotheres pubescens a Junior Synonym of T. margarita. - The comparison between the morphology of the subadult females of T. margarita and the description of P. pubescens noted by Holmes (1864) indicates that these two putatively different species are almost identical. Discrepancies between my description and that of Holmes are in the walking legs and the palp of the third maxilliped. Holmes noted that the walking legs are subequal. However, I found that the relative length is 2 > 3 > 4 > 1, in decreasing order. The second leg is asymmetrical, the left dactylus being slightly longer than the right. With respect to the palp of the third maxilliped. Holmes reported that this consists of two articles, but I found three. The dactylus lies close along the ventral margin of the propodus and may be overlooked.

I considered that the above discrepancies concerning the symmetry/asymmetry of the second pair of walking legs arise because Holmes studied a hard-stage female and my description was based on a late posthardstage female (perhaps III or IV). I suspect that the differences noted in the relative length of the walking legs and the palp of the third maxilliped resulted from misinterpretations of the holotype of *P. pubescens.* Since the two species are similar in all other features, I propose that *P. pubescens* is a junior synonym of *T. margarita*, the older named species.

Subadult Male. — This is almost identical to the adult male figured by Campos-González and Campoy-Favela (1988). Differences were observed in the following features: carapace with very sparse or without velvety pubescence, frontal region with medial notch; walking legs relatively slender, and dactyli relatively longer; abdomen with lateral margins more parallel; and gonopods similar but undifferentiated (Fig. 3a–c).

Morphological and Biological Remarks. -The finding of two subadult males, each living together with a subadult female, was the observation that permitted me to conclude that these specimens are postplanktonic stages of T. margarita. As noted above, the morphology of the male is almost identical in the subadult and adult stages. However, the morphology is different from that of the postplanktonic female stages. These subadult stages can be recognized as females, although they possess several masculine features which are lost only when the adult stage is reached. An objective identification of T. margarita can be made on the basis of the third maxilliped, the carapace regions, and, eventually, the second pair of walking legs. With respect to the third maxilliped, T. margarita possesses a spatulate propodus larger than the carpus and a narrow, spatulate dactylus which is inserted in the middle on the ventral margin of the propodus. These features are otherwise observed only in the Atlantic species T. mac*ulatus.* With respect to the carapace, T. margarita possesses gastric and cardiac regions that are separated from the hepatic and branchial regions by a depression; all of these regions are tumid (Rathbun, 1918; Wicksten, 1982; Campos-González, 1988; present study). These features are seen exclusively in T. margarita and T. maculatus. Finally, the asymmetry in length of the second pair of walking legs is a diagnostic feature of T. margarita. However, I recommend caution with the use of this character.

A retrospective analysis of the postplanktonic development of pinnotherid crabs, which included my unpublished observations for several Mexican species, permits me to infer that very young females of *T*. *margarita* (prehard- and hard-stage) possess symmetrical walking legs. This inference is based on the fact that males and females at the prehard- and hard-stages are almost identical, differing only in the abdominal appendages. The male of *T. margarita* possesses symmetrical walking legs.

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